## **Short Note**

## Auditory Health of Bowhead Whales (*Balaena mysticetus*) of the Bering-Chukchi-Beaufort Stock Based on Inner Ear Neuron Counts

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Human activities in the polar seas have increased noise pollution and altered the acoustic landscape of the ocean (Hildebrand, 2009; Stafford, 2013; Weilgart, 2013; Southall et al., 2019). Potential impacts from anthropogenic noise on marine animals can be studied in a variety of ways: by studying changes in behavior, by measuring physiological parameters, or by studying damage to the animals' anatomy. This last approach is taken here to examine hearing in bowhead whales (Balaena *mysticetus*) of the Bering-Chukchi-Beaufort stock (Baird & Bickham, 2021). This species spends its entire life near the edge of the sea ice in Arctic waters, migrating as the ice waxes and wanes (Citta et al., 2021). Bowheads of the Bering-Chukchi-Beaufort stock, the largest of the four stocks (Baird & Bickham, 2021), represent a significant portion of the global population. These whales may be impacted by effects related to climate change, such as increased industrial shipping, fishing, and oil and gas development, some of which produce potentially damaging noise levels (Blackwell & Thode, 2021; Moore et al., 2021).

Mysticete cetaceans use their ears to receive the low frequency vocalizations used for intraspecific communication (Edds-Walton, 1997). Interestingly, bowhead and humpback whales (Megaptera novaeangliae) are the only baleen whales to produce complex songs that change markedly with time (Stafford, 2022). Bowheads have been recorded producing vocalizations between 25 to 5,000 Hz (Ljungblad et al., 1982; Clark & Johnson, 1984; Cummings & Holliday, 1987; Würsig & Clark, 1993; Stafford et al., 2008; Clark et al., 2015). As audiograms are unavailable for any baleen whale species (Southall et al., 2019), mysticete hearing ranges must be assessed using other methods. Ketten (1994) estimated bowhead hearing to range from 600 to 32,000 Hz based on

analysis of cochlear geometry and estimated stiffness of the basilar membrane. Parks et al. (2007) estimated a hearing range of 10 to 22,000 Hz for the closely related North Atlantic right whale (*Eubalaena glacialis*; Gatesy & McGowen, 2021), using measurements of basilar membrane geometry and dimensions.

We examined the inner ear morphology of eight bowhead whales of varying ages focusing on a critical peripheral auditory structure, the spiral ganglion, residing in Rosenthal's canal. Of particular interest was the distribution of neuron cell bodies in the spiral ganglion. This ganglion is the initial neural structure of the sound pathway from the cochlea to the brain. The spiral ganglion is a long, narrow, spiral-shaped aggregation of neuron cell bodies that parallels the inner and outer hair cell bands of the cochlea, the part of the ear where sounds are transduced into nervous impulses. The neuron cell bodies in the spiral ganglion follow the tonotopic arrangement of the adjacent basilar membrane and organ of Corti. Restated non-technically, these structures are located in a snail-shell shaped organ (cochlea). The hair cell band, where sound waves are transduced into neural impulses, is arranged in a long band inside the cochlea in which higher frequencies are detected in the basal portion while progressively lower frequencies are detected toward the apex. The spiral ganglion parallels the hair cell band along the entire spiraled cochlea (Figure 1). Thus, loss of neuron cell bodies within the spiral ganglion may record evidence of past acoustic trauma in which the location of damaged or lost cells along the cochlea's length depends on the frequencies of traumatic exposure (Lurie et al., 1944; Schuknecht, 1974; Fredelius, 1988; Fredelius et al., 1988; Kujawa & Liberman, 2006, 2009).

The soft tissues of the inner ear are prone to rapid deterioration after death (Spoendlin &



**Figure 1.** *Balaena mysticetus* reconstructions of cochlea and Rosenthal's canal µCT scans; these show the bony labyrinth (red) and Rosenthal's canal (blue): (A & B) apical views of NSB-DWM 2012B15L, and (C & D) oblique views. (B) and (D) match (A) and (C), respectively, in orientation. (E) 3-D reconstruction of cochlea (NSB-DWM 2012B17R) cut virtually to show how cross-sectional areas of Rosenthal's canal were determined. Scale bar below (D) is for views (A) through (D). Figure adapted from Sensor (2017).

Schrott, 1988; Glueckert et al., 2005; Morell et al., 2022). Well-preserved cochleae from cetaceans are not commonly available for study because extracting these structures from a dead animal is difficult and is further complicated by legal and ethical issues related to the killing of cetaceans (Ramírez et al., 2020). These difficulties make the dataset of eight well-preserved samples presented herein an important addition to our understanding of cetacean ear histology and morphology. We examined spiral ganglion neuron density along the length of the cochlea within Rosenthal's canal of bowheads for the first time. Given our relatively large sample size, with a diversity of ages sampled, we hope to provide a baseline for expected spiral ganglion cell density. This initial baseline can potentially be used to evaluate individual whales within our sample for signs of unusually low auditory neuron density, indicating cell death, a condition which can be associated with acoustic trauma.

Bowhead whales are harvested in spring and fall by Iñupiat Alaskans in Utqiagvik, Alaska, when the whales migrate between the Bering, Chukchi, and Beaufort Seas (George et al., 2004). This hunt is permitted under the Endangered Species Act and the Marine Mammal Protection Act as part of the indigenous subsistence harvest. Petrosal (ear) bones are collected in collaboration with scientists from the Department of Wildlife Management of the North Slope Borough, Utqiagvik, Alaska (NSB-DWM) under NOAA-NMFS Permit 21386.

NSB-DWM specimen numbers assigned to samples are used in the text and figures, appended with an "R" or "L" to indicate the right or left petrosal. Petrosal bones from eight individual whales (Table 1) were sampled and fixed (for at least 3 wks) in 2.5% glutaraldehyde before additional processing. All samples were acquired within 12 h of the animal's death, with the sampling being done outside in temperatures never above 10°C and usually below freezing. Ages of each specimen were estimated using length of the longest baleen plate following Lubetkin et al. (2008, 2012). Specimens were scanned prior to dissection and decalcification using a µCT vivaCT 75 (SCANCO Medical, Brüttisellen, Switzerland). Reconstructions of the scans are used to guide subsequent dissections and to aid in the acquisition of canal morphometric parameters and sample location.

We followed a modified procedure of Sensor et al. (2015) who studied spiral ganglion morphology in beluga whales (*Delphinapterus leucas*). After fixation and  $\mu$ CT scanning, the stapes was removed to allow access to the oval window. Then, either a 0.1% thionin or 3% OsO4 solution was flushed through the scalae via the round and oval windows, allowing visualization of the bony labyrinth during subsequent dissection. The bone surrounding the cochlea of bowhead whales is considerably thicker than that of belugas, so excess bone was removed using a Foredom rotary tool, taking care not to damage the stained scalae. Specimens were demineralized in 10% EDTA

NSB-DWM	Sex	Body length (m)	Longest baleen plate length (cm)	Est. age
2010B15	F	12.50	267	32.0
2010B20	М	7.80	85	1.5
2011B3	F	17.50		
2011B8	F	8.40	131	3.0
2011B9	F	12.50	235	22.0
2012B15	М	8.40	85	1.5
2012B17	F	10.80	217	17.7
2012B18	F	9.40	155	5.0

**Table 1.** Bowhead whale (*Balaena mysticetus*) specimens examined for this study, including sex, body length, length of longest baleen plate, and estimated age (based on longest baleen plate length)

(pH 7.5) for 3 to 6 wks during which time periodic checks of the progress and endpoint determination were assessed with µCT scans. After demineralization, the remaining bone was removed to expose the scalae at which point dissection commenced at the apex of the cochlea and consisted of extracting wedge-shaped segments that included Rosenthal's canal, organ of Corti, and stria vascularis. The entirety of Rosenthal's canal with spiral ganglion was divided into approximately 15 segments that were extracted for histological serial sectioning. Individual segments were processed and embedded in paraffin using standard laboratory protocols. Serial sections (7 µm thick) were cut in a plane orthogonal to the long axis of Rosenthal's canal and stained with haematoxylin and eosin (H&E) for microscopic examination. For methodological reasons, sections from the basal regions of the cochlea were more likely to fall apart during histological processing resulting in fewer usable sections in this portion of the cochlea.

We chose four sections from each serially sectioned segment that were separated by four or five adjacent serial sections. Counts were performed on the photomicrographs and included only those cells in which the nucleus was visible in images acquired with a 10x objective. Given that spiral ganglion neurons have a nucleus that is larger than the section thickness, a nucleus is likely to be visible in several adjacent serial sections, which, if counted, could lead to an overcount of neurons. To account for this, we apply the Abercrombie correction as described by Hedreen (1998). It uses the section thickness and nucleus diameter to calculate a correction factor, a procedure previously applied to cetaceans (Wever et al., 1971, 1972; Parks et al., 2007). The final cell densities given in cells per linear mm of Rosenthal's canal are the counts of four individual sections, and these result

in an estimate for each segment (corrected for nucleus splitting). Cell density is thus estimated by extrapolating the linear density of the 7  $\mu$ m thick sections' density per mm. These data are plotted as the midpoint of each cochlear segment as located on the  $\mu$ CT scans of each specimen. In addition, we plot a composite of all individuals sampled by binning and averaging samples from each available 10% increment along Rosenthal's canal length.

The bowhead cochlea contains 2.25 whorls (Figure 1). The basilar membrane has a mean length of 43.4 mm, while Rosenthal's canal, residing closer to the modiolus, is shorter and consists of two whorls with a mean length of 41.2 mm. Neuron cell bodies (Figure 2) are usually oblate; the measured nuclei had a mean diameter (longest diameter visible in a cross-sectioned spiral ganglion) of 10.1  $\mu$ m (SD = 1.35). While types I and II spiral ganglion cell bodies could not be conclusively identified on histologic criteria, some of the smaller neurons occasionally encountered are morphologically consistent with descriptions of type II spiral ganglion cells. The ability to identify a nucleolus within the nucleus varied among sampled whales, possibly a preservation artifact.

We report numbers of spiral ganglion neuron cell bodies per linear mm of Rosenthal's canal (Figure 3A) from base to apex. The average number of spiral ganglion neuron bodies is 2,267.5 (SD = 319.7) per linear mm of Rosenthal's canal based on all segments and specimens. For each 10% increment of Rosenthal's canal, the average number of spiral ganglion cells per segment (shown graphically in Figure 3B) ranged between 1,880.2 and 3,016.6 cell bodies per mm. Spiral ganglion nuclei counts for all eight bowhead whale specimens are plotted in Figure 3A. Variation of counts within a segment and between segments of the same individual do occur, although no



**Figure 2.** Demineralized paraffin sections (7 µm), H&E stained, of Rosenthal's canal (NSB-DWM 2010B15R): (A) complete section of Rosenthal's canal, including surrounding bone, ganglion cell bodies, and nerve fibers entering the habenula perforata (to the right); and (B) close-up of spiral ganglion neuron cell bodies indicated by red box in (A); yellow arrows show selected spiral ganglion neuron cell nuclei, and small blue nuclei belong to the numerous glial cells present.



**Figure 3.** Results of spiral ganglion nuclei counts along the bowhead cochlea. The cell counts are reported as cells per linear mm along Rosenthal's canal and have been corrected for double counts resulting from split nuclei during sectioning. The counts are plotted against the percent distance from the cochlea base such that the most basal part is 1% and the apex is 100%. (A) Plot of all counts from all whales; and (B) plot showing means and standard deviations for all eight specimens (same data as A) within each 10% length increment along the cochlea, calculated from the average for each specimen available in each segment.

precipitous drop in cell density is observed for any specimen. Interestingly, our average spiral ganglion cell density of 2,267 cells per mm is similar to numbers reported for two toothed whales: around 2,500 spiral ganglion neuron cells per mm in the bottlenose dolphin (*Tursiops truncatus*) and 2,200 cells per mm for the pantropical spotted dolphin (*Stenella attenuata*) (Wever et al., 1971; Ketten, 1992).

Increased levels of industrial noise in the Arctic Ocean pose a threat to cetaceans (Moore et al., 2012, 2021). Acoustic trauma in the form of specific events or sustained exposure may consist of damage to the hair cells of the cochlea. When hair cells in the cochlea are damaged or die, the neurons which they communicate with are also subject to degeneration and death (Hurley et al., 2007; Henderson et al., 2008). This neural degeneration is not immediate and can take several weeks to years after hair cell death to be visible histologically (Lurie et al., 1944; Fredelius, 1988; Fredelius et al., 1988; Kujawa & Liberman, 2006; Houser, 2021), although minor signs of damage (e.g., vacuoles in the ganglion cells) can be seen within several hours after exposure (Wang et al., 2002).

Spiral ganglion cell density varies along the length of the cochlea in mammals of the same species but is not subject to large or rapid density changes in a healthy individual (e.g., Webster & Webster, 1981; Nadol, 1988). This condition may be the result of acoustic trauma at frequencies resolved around that location of the spiral ganglion, although maximal damage may occur at frequencies half an octave higher than the original exposure frequency (Cody & Johnstone, 1981). Other causes for such damage (e.g., normal aging, antibiotic use) that also lead to neuron loss are unlikely in our sample of mostly younger individuals. Acoustic trauma due to exposure to loud sounds is known to damage spiral ganglion neurons, and this damage can be observed in histological sections of the ganglion by the presence of areas of the ganglion lacking neurons and filled with connective (scar) tissue (Wang et al., 2002). If sharp drops in the density distribution of the spiral ganglion cells are observed, apoptosis of neurons is likely and may provide a record of acoustic damage.

Within our sample of bowheads of the Bering-Chukchi-Beaufort stock, no areas of anomalously low spiral ganglion cell densities were found within the cochleae investigated (Figure 3B). In addition, spiral ganglion cell densities show no apparent correlation (not figured) with the estimated age of the specimens examined, suggesting that the whales sampled were not old enough to exhibit age-related neuron loss at levels our methodology was sensitive enough to resolve. While we cannot be sure that all the whales studied by us did not have some level of anatomically documented hearing damage, two factors are not consistent with hearing damage. First, some of our individuals are extremely young, suggesting that they would have accumulated hearing damage at a very early age, before year one. Second, pronounced hearing damage in the spiral ganglion displays morphologically as areas of "scar tissue," lacking neuronal somata. Most of our individuals lack such areas altogether.

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